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# Elevational diversity of terrestrial rainforest herbs: when the whole is less than the sum of its parts

Sandra Willinghöfer · Daniele Cicuzza · Michael Kessler

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**Abstract** We studied the species richness of herbaceous terrestrial plant species along an elevational gradient at 250–2425 m a.s.l. in evergreen tropical forest in Central Sulawesi, Indonesia. We recorded 302 species belonging to 51 families. Ferns and lycophytes contributed 62% of the species, followed by monocots with 24% and dicots with 14%. Overall herb species richness did not show any particular relation with elevation, while the richness of ferns increased significantly with elevation, monocots did not show a pattern, and dicots showed a hump-shaped pattern with maximum richness at 1800 m. These patterns in turn were only partly reflected in the patterns of the individual plant families making up each group. The independence of different taxa was also reflected in their relationships to environmental factors (temperature, precipitation, and area): although, each single family was related to one or several factors, at the group level and at the overall

level these trends were lost. These results show that interpreting diversity at higher taxonomic level may overlook important information at the family level and raises the biologically intriguing question whether overall patterns of diversity result from a random accumulation of group-specific patterns or if there is some interaction between groups (e.g., via competition and niche-pre-emption).

**Keywords** Elevational gradient · Terrestrial herbs · Tropics · Diversity · Species richness · Sulawesi · Indonesia

## Introduction

Tropical rainforests are well known for their enormous plant and animal diversity, which is especially concentrated in mountain regions (Myers et al. 2000; Kreft and Jetz 2007). While the number of field studies on tropical plant diversity is constantly increasing, this research effort is taxonomically and ecologically unevenly distributed, focussing on trees at the expense of other life forms (lianas, shrubs, terrestrial, and epiphytic herbs) (Linares-Palomino et al. 2009). Although, terrestrial herbs are recognized as an important component in tropical plant communities (Gentry 1995; Gentry and Dodson 1987; Linares-Palomino et al. 2009), there are few quantitative studies of the diversity of tropical herbs. The terrestrial

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layer of herbaceous plant species in tropical forests plays an important role in light limitation and space competition for seedling and juvenile trees (Tsvuura et al. 2010), influencing tree regeneration and forest dynamics (Condit et al. 2000), but there is very little data on the diversity of terrestrial herb assemblages (e.g., Poulsen and Pendry 1995). Along tropical elevational gradients, for example, there are dozens of studies on the diversity of trees (e.g., Kitayama 1992) and a lesser number on lianas (Homeier et al. 2010), ferns (Kluge et al. 2006; Kessler 2000, Kessler et al. 2011) and epiphytes (Krömer et al. 2005; Cardelús et al. 2006), but we are aware of only a handful of studies including terrestrial herbs, although none of these specifically focuses on herbs. Moreover, these studies have all recovered different elevational species richness patterns: Poulsen and Pendry (1995) documented a U-shaped pattern along a short elevational gradient (200–850 m) in Borneo, Poulsen et al. (2005) a monotonic decline between 770 and 1520 m in central Africa, Grytnes and Beaman (2006) a hump-shaped pattern along an extensive gradient (0–4094 m) in Borneo, and Desalegn and Beierkuhnlein (2010) a roughly monotonic increase with elevation in Ethiopia (1200–2700 m). Thus, little is known on how the diversity and community composition of forest herbs change with elevation, whether there is any generality to them, and if these patterns correspond with those of other life forms.

Elevational gradients offer an outstanding opportunity to study and understand patterns of biotic diversity because they represent reproducible environmental gradients that can be replicated across the globe (Lomolino 2001; McCain 2009). Approximately, half of all case studies across a wide range of taxa show hump-shaped richness patterns with maximum richness at an intermediate point of the gradient, with the remainder of the studies including monotonic increases or decreases as well as roughly constant numbers (Rahbek 1995, 2005; McCain 2007, 2009). The causes for these different patterns are largely unknown but are often taxon-specific and depend on the spatial extent as well as the geographical location of the gradients (Rahbek 2005; Kessler et al. 2011).

A large number of partly non-exclusive explanations have been proposed for taxon-specific elevational richness patterns, including (1) current climatic variables such as temperature and humidity (Heaney

2001; Kessler 2001; Bhattarai et al. 2004) which in turn determine energy availability and ecosystem productivity (Hawkins et al. 2003; Currie et al. 2004), (2) spatial aspects including regional area size (Rosenzweig and Ziv 1999) and geometric constraints (Colwell et al. 2004; Grytnes et al. 2008), (3) historical and evolutionary processes (Ricklefs 2004), and (4) biotic processes such as the Rapoport rescue hypothesis (Stevens 1989) or source-sink effects (Grytnes 2003; Kessler 2009). All of these factors may covary with both hump-shaped and linear species richness patterns, and discrimination between them is frequently difficult, especially due to a lack of relevant ecological data. Despite these limitations, there is increasing consensus that there are close links between species richness and climatic factors, and that factors such as area, geometric constraints and population-level processes at best modify the climate-dependent patterns (Currie and Kerr 2008; McCain 2009; Kessler et al. 2011).

The objective of this study was to document the patterns of species richness of terrestrial forest herbs along an elevational gradient on the island of Sulawesi in Indonesia and to identify possible correlations with environmental factors. Specifically, we asked the following questions: (1) How does terrestrial herbaceous species richness change along the elevational gradient? (2) Do different taxonomic groups show similar patterns? and (3) Which are the environmental and spatial factors correlated with herbaceous species richness?

## Materials and methods

### Study sites and field sampling

The study was conducted in and around the Lore Lindu National Park (LLNP) in Central Sulawesi (Indonesia). The park encompasses an elevational gradient from 200 to 2509 m a.s.l., with about 90% of the area above 1000 m. Precipitation ranges from 2000 to 4000 mm and mean annual temperatures from 26 to 31°C (The Nature Conservancy, 2004).

Field sampling was conducted at eight different sites covering elevations between 250 and 2425 m: Saluki, Mount Nokilalaki (subdivided into 4 elevational belts), Pono, Bariri, and Mount Rorekatimbu (Table 1, Fig. 1). The highest peak in Central

**Table 1** Overview of the study sites, with information on elevation and climate

Study site	Coordinates	Elevation (m)	Mean annual precipitation (mm)	Mean annual temperature (°C)
Saluki	1°18'25.21" S 119°57'58.20" E	250	1890	24.3
Saluki	1°18'19.64" S 119°58'59.86" E	300	1890	24.3
Saluki	1°17'46.60" S 119°58'33.27" E	350	1890	24.3
Pono	1°29'20.54" S 120°3'30.25" E	850	1895	21.3
Pono	1°29'6.94" S 120°3'17.11" E	900	1895	21.3
Pono	1°29'41.76" S 120°3'45.29" E	1120	1895	21.3
Nokilalaki	1° 13' 21.15" S 120° 9'18.54" E	1200	1820	19.6
Nokilalaki	1°13'31.88" S 120°9'16.21" E	1200	1820	19.6
Nokilalaki	1°13'41.14" S 120°9'15.24" E	1265	1820	19.6
Bariri	1°39'48.34" S 120°10'15.78" E	1400	1975	19.1
Bariri	1°39'38.48" S 120°10'11.69" E	1400	1975	19.1
Bariri	1°39'28.35" S 120°10'2.32" E	1400	1975	19.1
Nokilalaki	1°13'80.95" S 120°9'1.18" E	1400	1840	18.9
Nokilalaki	1°13'48.02" S 120°9'5.01" E	1400	1840	18.9
Nokilalaki	1°14'4.12" S 120°9'18.51" E	1490	1840	18.9
Nokilalaki	1°14'21.87" S 120°9'20.87" E	1800	1875	18.3
Nokilalaki	1°14'35.48" S 120°8'56.25" E	1800	1875	18.3
Nokilalaki	1°14'46.63" S 120°9'14.79" E	1880	1875	18.3
Nokilalaki	1°14'45.32" S 120°9'87.21" E	2200	1940	17.0
Rorekatimbu	1°16'21.34" S 120°18'75.81" E	2350	2132	14.1
Rorekatimbu	1°16'42.66" S 120°18'34.14" E	2400	2132	14.1
Rorekatimbu	1°16'52.47" S 120°18'33.41" E	2425	2132	14.1

Sulawesi is Mount Rorekatimbu (2509 m), hence our transect covered almost the entire elevational range. Sampling was conducted in 2006 at Bariri and from February to April 2008 at the remaining sites. We established a set of three study transects at each locality, with the exception of the summit of Mount Nokilalaki, where only a single transect was placed, resulting in a total of 22 transects (Table 1). Each transect consisted of 12 plots of 5 m × 5 m each, separated by intervals of 35 m from each other, resulting in a total transect length of 445 m. The area of each transect was 300 m<sup>2</sup> for a total area of 6600 m<sup>2</sup> for the whole study. Transects were placed in mature forest, avoiding gaps and other anthropogenic and natural disturbances, water-logged soils or open rock faces. Transects were located following the contour lines to avoid variation in elevation within the transect span.

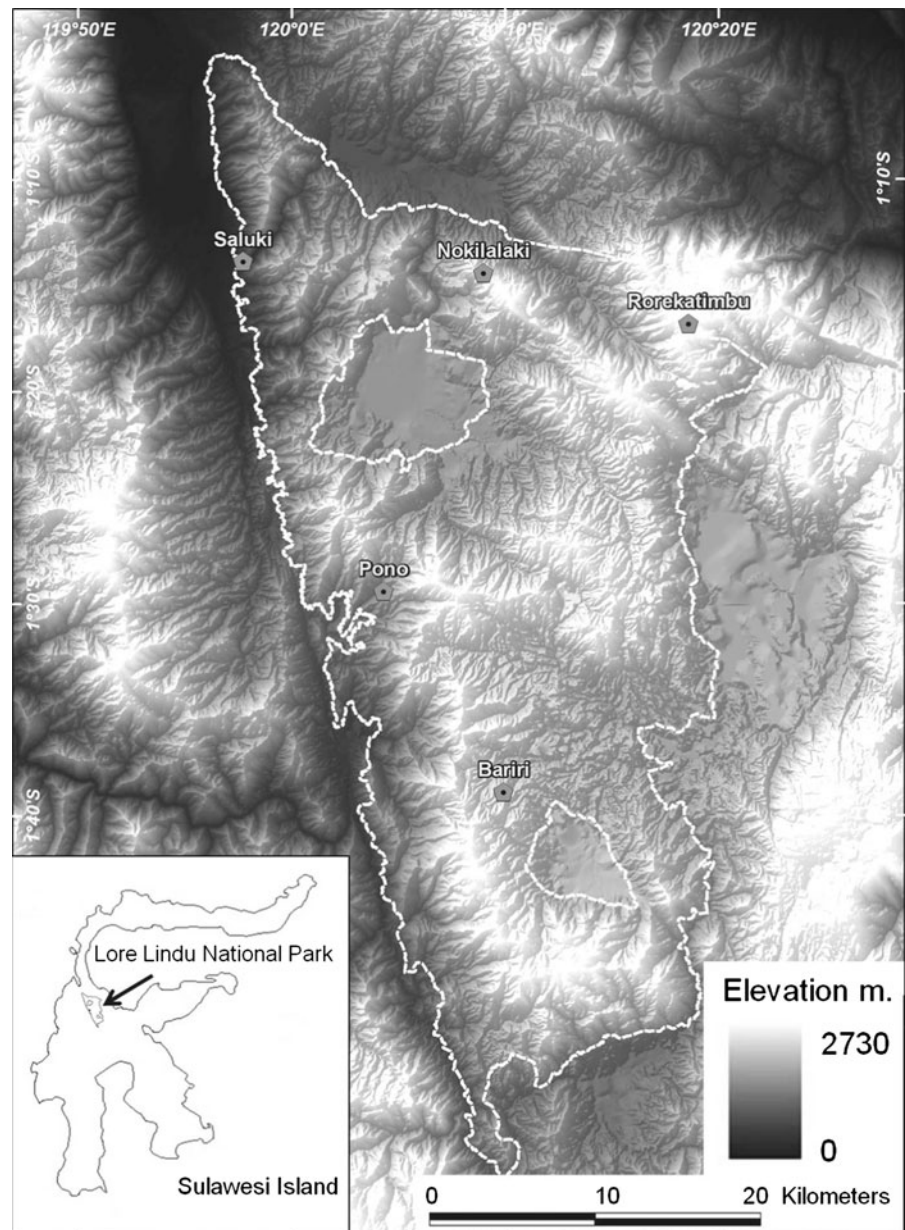
One possible concern for this study is that sampling took place on several mountains, rather than across the full elevational gradient of a single mountain. This

was necessary because of high rates of deforestation in the study region and limited accessibility due to the steep terrain. However, the three transects conducted at the two localities (Bariri and Nokilalaki) at 1400 m have identical species numbers, suggesting that our study sites are regionally representative.

In each study plot, all terrestrial herbaceous species as well as elevation (measured with a GARMIN GPS) and slope were recorded. All plant species were collected, subsequently identified where possible to species level, and finally deposited in the following herbaria: Göttingen (GOET), Bogoriense Bogor (BO), Celebense Palu (CEB), Leiden (L), Zurich (Z), and Berkeley (UC; ferns only).

As environmental variables, we included mean annual temperature, mean annual precipitation, and land surface area. Climatic parameters for each study site were extracted from WorldClim (Hijmans et al. 2006). Area was evaluated by estimating the island surface of Sulawesi subdivided by elevational belts: 0–500, 501–1000, 1001–1500, 1501–2000, 2001–2500,

**Fig. 1** Location of the protected area and the five focus study area, in the small quadrate the map of the Sulawesi Island with the border of the Lore Lindu National Park in central Sulawesi



and 2501–3000 m. We did not analyse variations of species numbers at the level of plots within transects across the elevational gradient because plots within a transect are spatially autocorrelated.

#### Statistical analyses

For the analyses, we calculated the mean number of species per plot for the following taxonomic groups: all terrestrial herbaceous plant species together,

separated into three major taxonomic groups (ferns and lycophytes, henceforth called ferns; monocots; dicots), and for the three most species rich families of each of the major groups (Table 2). Although, not monophyletic, we treated ferns and lycophytes as a single group due to the low number of lycophytes and the physiological and ecological similarities between the groups. Likewise, dicots were treated as a group because our sample mainly included eudicots and very few basal dicots. In an earlier phase of the analyses, we



**Table 2** Results of the multiple regression models relating the species richness of our study groups to three environmental factors

Taxa/Families	Area	Mean annual temperature	Mean annual precipitation
Total species	0.82 (*; –)	0.37	0.19
Ferns	1 (**)	0.44	1 (**; +)
Aspleniaceae	1	0.27	–
Dryopteridaceae	0.46	0.32	–
Polypodiaceae	0.68	0.32	0.2
Monocots	0.3	1 (*; +)	–
Araceae	0.3	1	0.42
Orchidaceae	–	–	–
Zingiberaceae	0.68	0.32	–
Dicots	0.36	0.64 (**)	1 (***; –)
Urticaceae	0.22	0.34	0.83
Gesneriaceae	0.28	1	1
Begoniaceae	0.44	0.56	1

Presented is the relative variable importance (RVI) for each environmental factor and the species richness of our study groups. Values close to 1 show that the respective factor played an important role in all competing multiple regression models with AIC values <2 from the best model, values close to 0 that the factor was unimportant in these models. *Dashes* reveal cases where the factors were not included in the models. For each group we present the best model and the directions of correlation, representing by \* the *P* value of each factor included in the model and (+) positive and (–) the correlation direction

\*  $P < 0.05$ , \*\*  $P < 0.01$ , \*\*\*  $P < 0.001$

also calculated total numbers of species per plot as well as estimated total species richness per plot applying the Chao2 richness estimator using EstimateS (Colwell 2008). As the results of all three levels of species richness were essentially identical, we only report the mean species number per plot.

To assess the elevational richness patterns of each group, simple linear and polynomial regression models were used to correlate the richness with elevation. Next, stepwise multiple linear regression analysis was used to select the combination of environmental variables that was most strongly related to herbaceous species richness. Elevation was not included as a variable in these analyses because it does not directly influence species richness (Körner 2000) and because it is closely correlated to temperature. For model selection, we used the Akaike Information Criterion (AIC), which incorporates the maximized log-likelihood of the model and a term that penalizes models

with greater complexity (Johnson and Omland 2004). The model with the lowest AIC value is considered as the best fitting model (Johnson and Omland 2004), but when the AIC difference between competing models is small, choosing a single “best model” may lead to a faulty interpretation (Wagenmakers and Farrell 2004). Models with  $\Delta\text{AIC} < 2$  all have a substantial support, while there is less support when  $\Delta\text{AIC} > 4$  (Burnham and Anderson 2002). Based on  $\Delta\text{AIC}$ , the Akaike weight quantifies that a given model is better than the next model within the set of all models. Weighting the different models, we estimated the relative variable importance (RVI) across all models by summing the weights of all competing models including this variable (Burnham and Anderson 2002), and the sums for the variables can then be compared. All analyses were conducted with R version 2.10 (R Development Core Team 2010), with additional functions provided by the R package vegan (Oksanen et al. 2007).

## Results

In total, we recorded 302 terrestrial herbaceous plant species belonging to 51 families. Of these, 163 were identified to species level (54%), 97 to genus level (32%), and 42 to family level (14%). Ferns and lycophytes contributed 62% of the species and 41% of the families, monocots 24% of the species and 22% of the families, and dicots 14% of the species and 37% of the families. At the family level, the most species rich families were: (1) Polypodiaceae (29 species), Aspleniaceae (28), and Dryopteridaceae (16), for ferns, (2) Araceae (28), Orchidaceae (19), and Zingiberaceae (14) for monocots, and (3) Gesneriaceae (8), Begoniaceae (5) and Urticaceae (5), for dicots.

Among the environmental variables, temperature and elevation ( $R = -0.98$ ,  $P < 0.001$ ) as well the area and elevation ( $R = -0.88$ ,  $P < 0.001$ ) and precipitation and elevation ( $R = 0.56$ ,  $P = 0.006$ ) were correlated with each other. Area was significantly correlated to temperature ( $R = 0.85$ ,  $P < 0.001$ ) but not to precipitation ( $R = -0.29$ ,  $P = 0.195$ ) (Suppl. Mat. Fig. S1).

The mean number of species per plot of all herbaceous taxa combined was, at best, weakly related to elevation (Fig. 2). However, when we analyzed the three main subgroups separately, we recovered distinct patterns for each of them. Fern richness increased

significantly with elevation ( $R = 0.60$ ,  $P < 0.001$ ) while monocots evidenced no clear elevational trend ( $R = 0.15$ ,  $P = 177.0077$ ), and dicots exhibited a hump-shaped pattern with highest richness at about 1800 m (Fig. 2). When we further considered the three most species-rich families per major taxonomic group, we also recovered distinct patterns. Among ferns, the species richness of Dryopteridaceae ( $R = 180.028$ ,  $P = 0.013$ ), Aspleniaceae ( $R = 0.27$ ,  $P = 0.013$ ), and Polypodiaceae ( $R = 0.20$ ,  $P = 0.036$ ) all increased with elevation (Fig. 2), in accordance with the general pattern for all ferns. Among monocots, Araceae ( $R = 0.07$ ,  $P < 0.001$ ) and Orchidaceae ( $R = 0.71$ ,  $P = 0.001$ ) showed decreasing richness with elevation, whereas that of Zingiberaceae increased ( $R = 0.27$ ,  $P = 0.014$ ) (Fig. 2). Finally, among dicots, Urticaceae showed a significant decrease ( $R = 0.27$ ,  $P = 0.013$ ), Gesneriaceae a significant increase ( $R = 0.55$ ,  $P < 0.001$ ) and Begoniaceae a non-significant pattern ( $R = 0.05$ ,  $P = 0.331$ ) (Fig. 2).

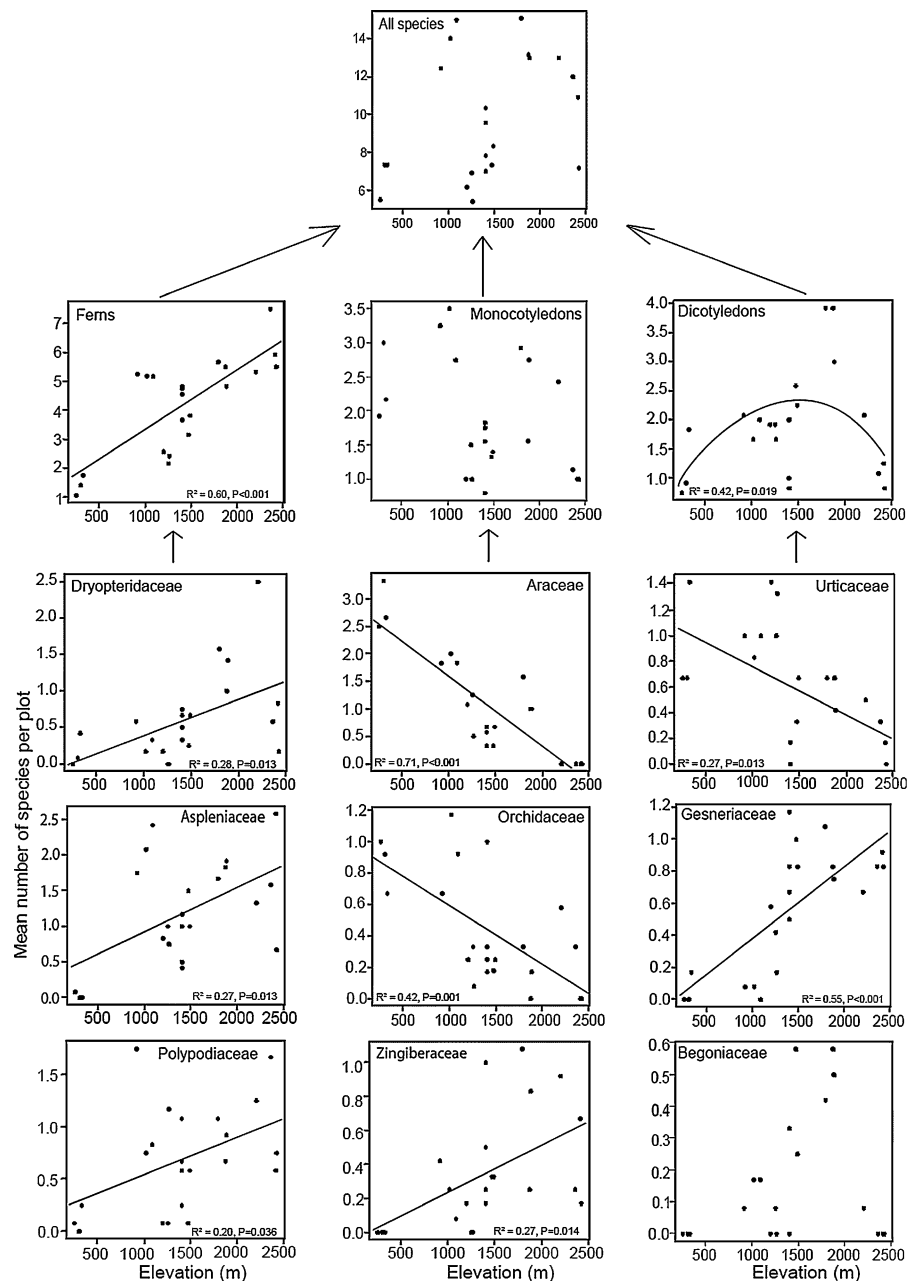
When we used multiple regression models to assess the explanatory power, using the relative variable importance (RVI) analysis using Akaike weights, the overall herb richness showed twice as high RVI values, for area than for mean annual temperature and four times higher than for mean annual precipitation (Table 2; Fig. 3). For ferns, area and precipitation had equally high RVI values about double that of temperature. At the family level, the species richness for each of the three most important families, Aspleniaceae, Dryopteridaceae, and Polypodiaceae, was related most strongly to area, followed by temperature. Only the model for Polypodiaceae included the precipitation factor, which had a very low RVI value. The overall pattern of species richness for monocots was related to temperature, followed by area; at the family level Araceae were related to temperature followed by precipitation and area, while the richness of Zingiberaceae species was related to area and temperature. In contrast, Orchidaceae were not related to any of the three factors. The overall dicot pattern showed the highest RVI value for precipitation followed by temperature and area. Urticaceae were supported by precipitation and less by temperature and area, Gesneriaceae were equally supported by precipitation and temperature, and less by area, in conclusion Begoniaceae by precipitation followed by temperature and area (Table 2, S1).

A major concern is the locality of Pono (1100 m) which has a particularly high diversity of herbaceous species and strongly influences the overall results. Despite noting this high diversity already during field work, we are unable to provide any convincing explanation at this point. Probably, local ecological conditions are involved, since nearby localities had much lower fern diversity (D. Karger and M. Kessler, unpublished data). We refrained from excluding the locality of Pono, however, because it was selected a priori based on the same criteria as the other sites and its exclusion solely on the basis of a lack of fit to the overall pattern would be subjective.

## Discussion

For each of our three initial research questions, we obtained distinct answers: although, total terrestrial herbaceous plant richness did not show a significant change with elevation (question 1), when we analysed the major taxonomic groups and families independently, most of them showed clear and often contrasting patterns (2), in many cases related to different sets of environmental factors (3). Or, in other words, the indistinct overall pattern resulted from the accumulation of distinct group-specific patterns. The overall lack of a clear elevational richness pattern for terrestrial herbs parallels the results from New Zealand forests (Ohlemüller and Wilson 2000) but contrasts with other studies, such as a U-shaped pattern found in Borneo (200–850 m) (Poulsen and Pendry 1995), a monotonic decline between 770 and 1520 m in central Africa (Poulsen et al. 2005), a hump-shaped pattern from sea level to 4094 m in Borneo (Grytnes and Beaman 2006), and a roughly monotonic increase between 1200 and 2700 m in Ethiopia (Desalegn and Beierkuhnlein 2010). This complexity may partly be the result of the different elevational spans covered by the studies, but likely also reflects differences in the ecological conditions between the study regions. It may also be illustrative to compare the elevational gradient to the latitudinal pattern, where a recent study has shown that the richness of herbaceous angiosperm families shows a much less pronounced decline away from the equator than the family richness of trees (Hawkins et al. 2011). The authors of the latter study suggest that this may be because herbs have shorter generation times than trees

**Fig. 2** Regression relationships between the mean number of species per plot to elevation for all terrestrial herb species (*top*), the three major taxonomic groups (*2<sup>nd</sup> row*) and the three most species rich families in each of these (*bottom three rows*)

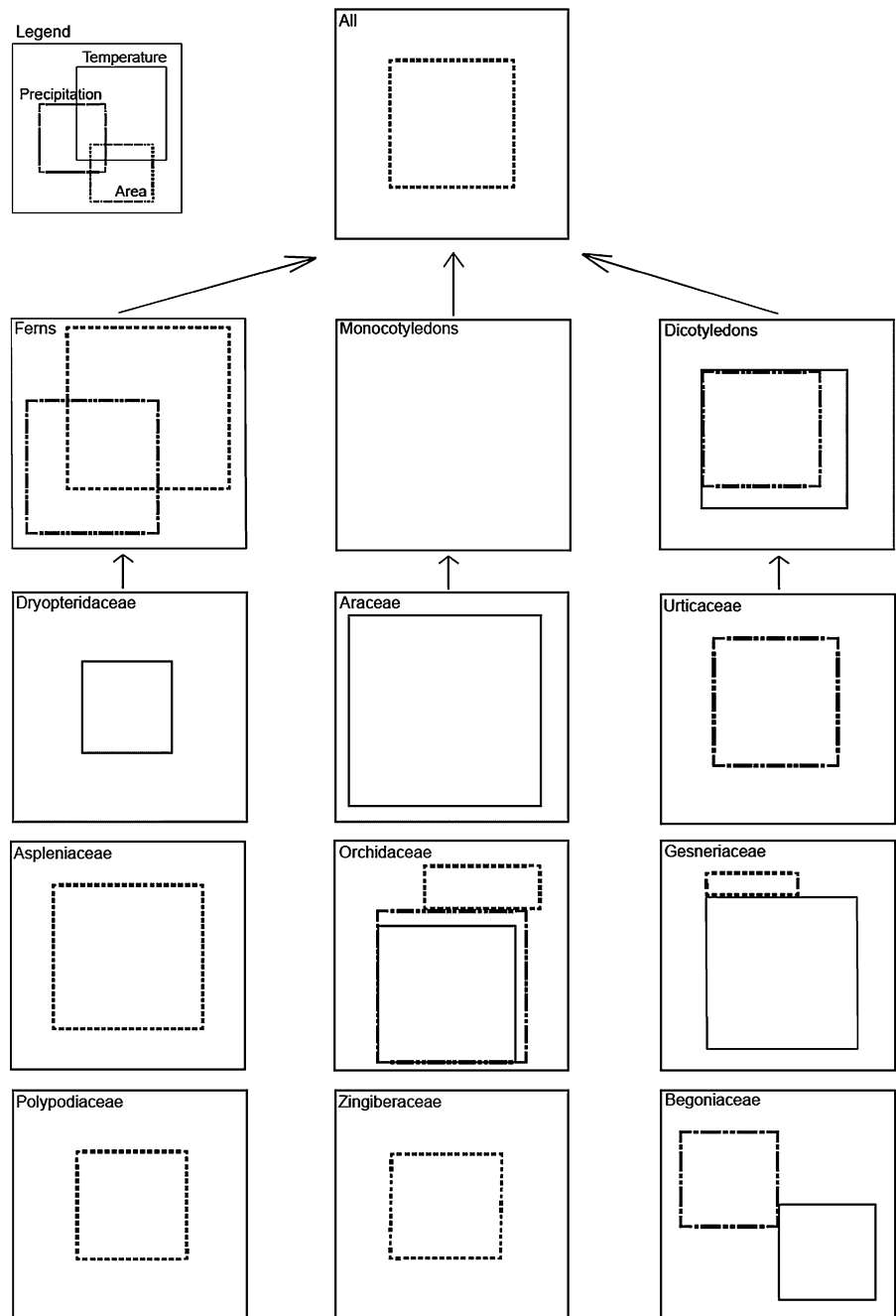


and are morphologically more flexible in their adaptations to low temperatures, enabling them to more quickly diversify at higher latitudes. In our study region, tree richness declines roughly constantly with elevation (Culmsee and Pitopang 2009; Culmsee et al. 2011) whereas herb diversity does not, pointing to a situation similar to that along the latitudinal gradient and suggesting that a similar mechanism may be at play along both geographical gradients.

Yet, while there was no clear elevational richness pattern for herbs overall, the major groups and families did show distinct patterns, which raises two interrelated follow-up questions. First, what are the causes of these group-specific patterns? And second, is the fact that the addition of group-specific patterns results in an indistinct overall pattern a chance event, or do the groups interact in some way so that overall herb species richness is restricted to a certain upper bound?



**Fig. 3** Visualization of the explanatory power of the three environmental variables (mean annual temperature, mean annual precipitation, and area) on the species richness of all terrestrial herb species (*top*), the three major taxonomic groups (*2<sup>nd</sup> row*), and the three most species rich families in each of these (*bottom three rows*). The sizes of the boxes are proportional to the percentage of variance explained by each factor, with overlapping areas showing variation that cannot be assigned to an individual factor



Focusing first on the individual groups, terrestrial fern species richness increased with elevation overall as well as among the three most species rich families (Fig. 2). This is a typical pattern in tropical mountains, where species richness of ferns peaks between 1500 and 2500 m, as shown by a worldwide comparison of elevational fern transects (Kessler et al. 2011). Monocots showed no clear pattern overall, as a result

of the addition of family-specific patterns of a decrease in Araceae and Orchidaceae, and an increase in Zingiberaceae. Araceae are well known to be best represented in humid lowland tropical forests and to decrease in their richness with decreasing temperatures (Kessler 2001; Mayo et al. 1997). In the central Himalayas, regional richness of terrestrial orchids increases from the lowlands to a maximum at about

2000 m (Acharya et al. 2011), in parallel to our results at the local scale. These results are supported by our multiple regression model for the Araceae, which includes temperature as a significant factor, but not for the Orchidaceae (Table 2). Unfortunately, little is known about elevational richness patterns of Zingiberaceae. The dicots showed a hump-shaped pattern overall, resulting from a combination of decreasing (Urticaceae), increasing (Gesneriaceae), and indistinct (Begoniaceae) patterns. No comparable studies exist for any of these groups so that the generality of the patterns observed in this study cannot be assessed. However, we found patterns consistent with those groups for which data from previous studies are available (ferns, aroids, and orchids), which suggests that findings from our study may be representative for other groups as well.

In the regression models, the overall dicot richness as well as that of Gesneriaceae and Begoniaceae decreased with temperature (Table 2). Precipitation had a negative relationship with the richness of all dicots, Begoniaceae and Urticaceae, whereas the richness of Gesneriaceae increased with the precipitation. Because of the paucity of studies on tropical forests herbs, we are unable to assess if these patterns are typical for these families and if they are representative for tropical environments. It is noteworthy, however, that several of our models included a negative relationship between species richness to area. While this result has statistical significance, it is biologically meaningless since there are no conceivable mechanisms by which increasing land surface area could reduce the species richness of a group. Most likely, this is a spurious result in which area captured part of the variation of species richness that is in effect accounted for by some ecological factor not measured by us (e.g., soil parameters, air humidity).

As detailed in the introduction, the covariance of explanatory factors along elevational gradients frequently makes it difficult to identify causal relationships. Despite these limitations, there are three non-exclusive major processes that may lead to the observed climate–species richness relationships.

First, the relationship may be determined by the physiological tolerances of the species involved. For example, high temperatures and low air humidity have repeatedly been proposed as limiting fern diversity in lowland tropical forests (Bhattarai et al. 2004; Kessler 2001; Kluge et al. 2006), and there is increasing

evidence that ferns are less capable of optimizing their water-use efficiency than angiosperms (Brodribb and Holbrook 2004; Brodribb et al. 2009). Furthermore, the majority of modern ferns have very sensitive photoreceptors (Doi and Shimazaki 2008). This appears to limit the productivity and competitive ability of many ferns and perhaps concentrates them in more shady and humid environments such as mossy mountain forests. Globally, diversity of ferns declines more strongly toward arid and cold climatic conditions than does that of angiosperms (Kreft et al. 2010), further suggesting that ferns are physiologically less adaptable. Similar arguments could be made for each of the other taxa, but because the physiologically most suitable climatic conditions are often deduced from where species richness is highest, there is always a risk of circular argumentation.

Second, there may also be an indirect effect of climate via ecosystem productivity (Lieth 1975; Currie et al. 2004) and hence the energy available for plant growth and development. Evans et al. (2005) proposed a number of mechanisms by which higher productivity can lead to higher species richness, e.g., because species are able to use more narrowly delimited niches. Unfortunately, we are currently unable to test these hypotheses because of the close covariance of productivity to climate, and because we lack productivity measures that are independent of climatic data. Furthermore, we do not know what proportion of the overall ecosystem productivity is taken up by the terrestrial herb assemblages and the individual groups at a given site and elevation.

Third, the high species richness of different groups at different elevations may be an evolutionary legacy of longer lineage ages, or of higher speciation or lower extinction rates under certain climatic conditions (Jablonski et al. 2006; Kozak and Wiens 2010), as has been suggested for the latitudinal pattern of the richness of herbaceous angiosperm families (Hawkins et al. 2011). Testing these hypotheses will require highly resolved and dated phylogenies, which are currently unavailable for our study groups and are generally limited in regions where plant taxonomies are poorly known, such as Sulawesi.

These various processes may have different impacts at different taxonomic levels, which bring us to the question of the causes. Ill-defined overall elevational richness patterns of plants resulting from the addition of distinct group-specific patterns have

previously been documented by Bhattarai and Vetaas (2003) in Nepal and Desalegn and Beierkuhnlein (2010) in Ethiopia, suggesting that the pattern observed in this study may be common in tropical mountains. However, Sánchez-González and López-Mata (2005) found congruent hump-shaped richness patterns for all plants and major groups in Mexico.

We can conceive two fundamentally different ways in which group-specific richness patterns may be added up. First, the individual groups may be independent of each other so that the indistinct overall pattern may simply be result of the random addition of the group-specific patterns. Second, overall herb species richness at a given elevation may be limited by space or resource availability (Bartels and Chen 2010). In the case that such an upper bound exists, species richness of a given lower-level taxonomic group would not be independent from the diversity of other groups. These hypotheses could be tested experimentally by, e.g., partly removing the herb vegetation from selected plots and observing the possible invasion by species previously absent. Another option would be to compare biogeographically disparate elevational transects along which the composition of, e.g. monocot families, varies, so that the intensity of interfamilial competition would shift. Clearly, species richness patterns of tropical herb species have been largely neglected so far but, as shown in this study, represent a potentially highly interesting field of research that may complement the extensive research conducted especially on trees.

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